Watsonia, **8**, 237–261 (1971).

The *Ranunculus acris* L. complex in Europe

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ABSTRACT

The geographical variation of the *Ranunculus acris* L. complex within Europe has been examined. The following taxa are recognised in this present work:

Ranunculus granatensis Boiss.
R. strigulosus Schur
R. acris L. *sensu stricto* subsp. *acris* var. *acris*
var. ***villosus*** (Drabble) S. M. Coles, **comb. et stat. nov.**
var. *pumilus* Wahlenb.
subsp. *borealis* (Trautv.) Nyman
subsp. *friesanus* (Jord.) Rouy & Fouc. var. *friesanus*
var. ***pyrenaeus*** S. M. Coles, **var. nov.**

R. granatensis and *R. strigulosus* have a restricted distribution and are relatively uniform in appearance. *R. acris sensu stricto* occurs over most of Europe and is a very variable plant. The main clinal variation in *R. acris* is in an east-west direction. *R. acris* subsp. *friesanus* forms no part of this variational pattern although its distribution is completely overlapped by that of subsp. *acris*.

INTRODUCTION

The plants investigated in this study are those included in *Ranunculus acris* L. as defined by Tutin (1964). *R. acris* L. *sensu stricto* in the present study excludes *R. acris* subsp. *granatensis* (Boiss.) Nyman and subsp. *strigulosus* (Schur) Hyl., which are given specific status.

The *R. acris* complex belongs to the section Ranunculus of the subgenus Ranunculus. It can be separated from most other European species of this section by having a terete pedicel, patent sepals and a glabrous receptacle. The diploid chromosome number of *R. acris* L. *sensu stricto* is 14; within the genus a basic chromosome number of 8 is more common than one of 7. *R. serbicus* Vis. ($2n=28$) is generally held to be a closely related species and probably merits inclusion within the complex, but it has not been considered here.

R. acris sensu lato is common over the whole of central and northern Europe including the British Isles, the Faeroes and Iceland. It also occurs in Greenland, but there has been some dispute as to whether it is truly native. Herbarium material examined from the south and east coasts of Greenland could not be distinguished from plants which have been introduced into Spitsbergen and N. America. The distribution of the complex is more limited in southern Europe. It is absent from Portugal; in Spain it only occurs in the north, east and south-east; it extends into Morocco. In Italy, material has been seen only as far south as Lat. 42°N. In the Balkan Peninsula it extends as far south as Albania and the Makedhonia region of Greece (Fig. 1). The distribution of the complex extends eastwards through Siberia and a series of forms is to be found in eastern Asia. It has been introduced into many of the temperate parts of the world, such as New Zealand, S. Africa and N. America; in the last it has spread in some regions with amazing rapidity (Benson 1948).

Details of the ecology of *R. acris* are given by Harper (1957). It is tolerant of a wide range of habitats, and is widespread over most of its range. One of its main limiting factors appears to be that of the water content of the soil. It is not markedly calcicole or calcifuge, although it does appear to be limited by a very low base-status.

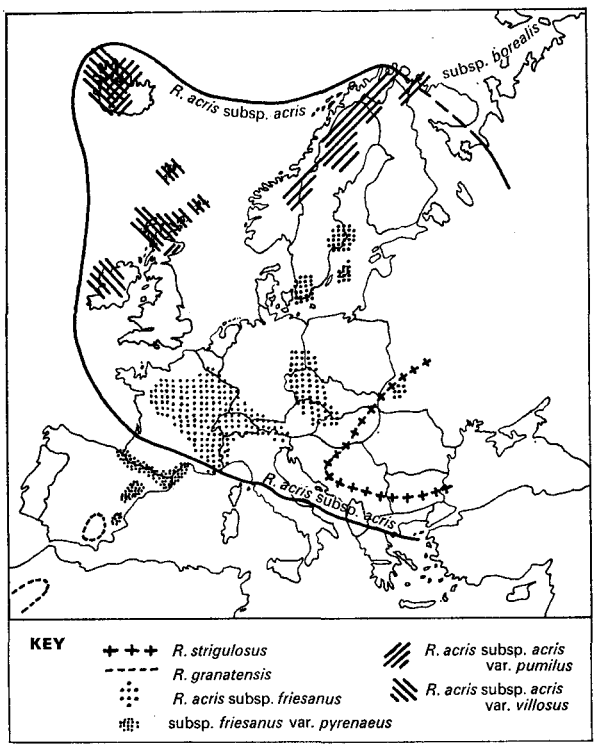

FIGURE 1. Distribution in Europe of the taxa recognised; based only on the material examined during this study.

Abnormalities of both the floral and vegetative parts of the plant are common. Some abnormalities of the flower can transform characters usually held as safe diagnostic characters of the complex. They may result, for example, in hairs being found on the receptacle or on the achenes. Gynodimorphism commonly occurs in the complex. All grades from functionally female to normal hermaphrodite flowers occur. Although there seems to be genetical control of these flower-types, fluctuations of types within a single plant are common (Marsden-Jones & Turrill 1929, 1935).

MATERIALS AND METHODS

This study was largely based on herbarium material from the following herbaria: British Museum (**BM**), Cambridge (**CGE**), Copenhagen (**C**), Edinburgh (**E**), Florence (**FI**), Kew (**K**), Leicester (**LTR**), Leningrad (**LE**), Liverpool (**LIVU**), Paris (**P**), Stockholm (**S**), Vienna (**W**).

The herbarium material was supplemented wherever possible by living material. Unfortunately living plants of *R. acris* subsp. *acris* and subsp. *friesanus* only could be obtained. The plants, from over fifty localities in the British Isles and from sixty localities on the Continent, were grown for periods of at least one year.

Characters were investigated from as many parts of the plant as possible. The following were found to be of most value: type of rootstock, shape of leaves, type of hair cover, and form of achenes. A detailed evaluation of characters and of the variations found within them, is given after a summary of the recognised taxa.

THE NOMENCLATURE AND SUMMARY OF THE CHARACTERISTICS OF THE RECOGNISED TAXA

Previous names which have been used in connection with plants belonging to this complex are very numerous (*Index Kewensis* lists over forty at specific level). Many of the names appear to have been used only by their authors and their descriptions give no clear idea of the taxon referred to, and where type material was seen it usually showed that the names were merely referable to plants which were parts of clines or which were showing seasonal variations. The synonyms given here include only names which have been commonly used by workers other than their authors. A fuller account of nomenclature has been given by Coles (1968).

The species category has been used where there are distinct, 'major', morphological discontinuities. The category of subspecies has been used to cover groups of plants from geographical regions which show 'major' morphological differences from other subspecies, but where there is also an array of intermediate types present. The category of variety has been used where the taxa have a geographical or ecological basis, but the morphological differences are not so great.

R. GRANATENSIS Boiss., Diagn. Pl. Or. Nov., Ser. 2, vol. 3 (1): 8 (1853).
R. atlanticus Ball, J. Bot., Lond., **11**: 296 (1873).
R. acris subsp. *granatensis* (Boiss.) Nyman, Consp., 12 (1878).
R. acris var. *atlanticus* (Ball) Maire, Flore de l'Afrique du Nord, vol. 11: 162 (1964).

R. STRIGULOSUS Schur, Enum. Pl. Transs., 17 (1866).
R. malocophyllus Schur, Enum. Pl. Transs., 16 (1866).
R. csatoi Schur, Verh. naturf. Ver. Brünn, **17**: 46 (1876).
R. acris subsp. *strigulosus* (Schur) Hyl., Symb. bot. upsal., 7: 1 (1943).

R. granatensis and *R. strigulosus* are both very distinct from any other taxa within the complex. *R. granatensis* is probably completely geographically isolated from the rest of the complex, and no intermediates with any other forms of the complex were seen. The plants of *R. granatensis* from Morocco appear similar to those of southern Spain, but only very poor material was seen. The distribution of *R. strigulosus* is overlapped by *R. acris* subsp. *acris*, but the only intermediate plants which were seen came from a single region in south-west Ukraine. These plants were exactly intermediate between the two supposed

parental types, and none were seen indicative of back-crossing to the parental species. This interpretation of the hybrid origin of these plants is in agreement with that of Hylander (1943).

R. granatensis and *R. strigulosus* are morphologically more closely related to each other than to *R. acris*. They are completely distinct from one another in floral but not in vegetative characters, although they can frequently be separated on the latter characters alone. They both have rhizomatous rootstocks and broad-lobed leaves with few teeth. In both species the beaks of the achenes are straight or only curved, never hooked, but they are longer in *R. granatensis* than in *R. strigulosus*.

R. ACRIS L., Sp. Pl., 554 (1753).

This is a very variable species which is distributed over most of Europe. All the infraspecific taxa recognised within it are linked by intermediates which do not appear to be of a hybrid nature.

Subsp. ACRIS

R. acris L. f. *multifidus* DC., Reg. Veg. Syst. Nat., **1**: 278 (1817).
R. boreanus Jord., Obs. Pl. Crit., **6**: 19 (1847).
R. tomophyllus Jord., Diagn., 71 (1864).

This is the most widespread subspecies and the most variable. The main cline of variation in Europe is from west to east. Plants characteristic of the west have long hairs, which are patent or deflexed on the lower part of the stem and on the petioles. In the east the hairs are usually shorter and appressed. Also, in the western plants the achenes and petals are larger. Broadly-lobed leaves are commoner in the western plants.

Subsp. ACRIS var. VILLOSUS (Drabble) S. M. Coles, **comb. et stat. nov.**
R. acris var. *friesanus* (Jord.) Drabble forma *villosus* Drabble, Rep. botl Soc. Exch. Club Br. Isl., **9**: 472 (1930).

Plants of this variety occur in northern Scotland, Ireland, the Faeroes and Iceland. They are characterised by having broadly-lobed leaves, which have many hairs exceeding 1·2 mm on their upper surfaces. The hairs on the petioles are long, often deflexed and usually of an orange-brown colour. One or two plants approaching this condition have been seen from the west coast of Norway, but no plants typical of this variety have been seen from the mainland of Europe. Plants of this variety occur in the remoter parts of these islands, where the vegetation has been relatively little affected by agriculture. It is probable that this variety was previously more widespread but is losing its identity by hybridising with plants of var. *acris*. In other areas in Britain, e.g. Teesdale, which have been relatively little affected by modern agriculture, the plants typically have long, deflexed hairs, and to some extent approach var. *villosus*.

Subsp. ACRIS var. PUMILUS Wahlenb., Flora Lapp., 159 (1812).

Var. *pumilus* is characterised by having leaves which are shallowly lobed and which are glabrous in the spring. It occurs in Scandinavia, Iceland and the Cairngorms, Scotland. It is mainly confined to mountains where it often occurs in snow-patch habitats. Some of the plants examined from the extreme north of Scandinavia were intermediate in character between subsp. *acris* var. *pumilus* and subsp. *borealis*. Plants of these two taxa appear to form part of a stepped cline from the north-west to the north of Europe.

Subsp. BOREALIS (Trautv.) Nyman, Consp., 12 (1878).
R. borealis Trautv., Byull. mosk. Obshch. Isp˜t. Prir., **33**: 72 (1860).

Plants of this subspecies are characterised by their very shallowly lobed leaves, the petioles of which are usually covered by deflexed hairs which are always very fine. The description of subsp. *borealis* in *Flora Europaea* (Tutin 1964) covers both this subspecies and subsp. *acris* var. *pumilus*. Plants of subsp. *borealis* have only been examined from the arctic coast of Russia, and the nomenclature of these plants may need to be revised when the representatives of the complex in the Urals and in Siberia are examined.

Subsp. FRIESANUS (Jord.) Rouy & Fouc., Fl. Fr., **1**: 103 (1893).
R. friesanus Jord., Obs. Pl. Crit., **6**: 17 (1847).
R. nemorivagus Jord., Diagn., 74 (1864).

This subspecies forms no part of the clinal variation as seen in the rest of *R. acris sensu stricto*. It is the only taxon within this species which has a rhizome; it is also characterised by having broadly lobed leaves. Its centre of distribution, the mountains of eastern France and western Switzerland, is completely overlapped by that of subsp. *acris*. It may have been ecologically isolated in the past, but at the present time intermediates between it and subsp. *acris* are very numerous. It has been introduced into other parts of the continent, e.g. Sweden and Austria, and here too it seems to be hybridising with subsp. *acris*.

Subsp. FRIESANUS var. **PYRENAEUS** S. M. Coles, **var. nov.**

Caudex rhizomatosus. Folia plerumque anguste lobata. Pili petiolares semper adpressi, haud tenuissimi. Habitat in Pyrenaeis Montibus et in Hispania septentrionali et orientali.

Rootstock rhizomatous. Leaves usually narrowly lobed. Petiole-hairs always appressed, never very fine. Found in the Pyrenees and in northern and eastern Spain.

Holotype: Pont de Ravi, near Hospice de France, open place in damp beech wood, France (Haute Garonne), 26. VII. 1961, *E. K. Horwood* (**LTR**).

This variety occurs over a wide geographical area, where it appears to be the only form of *R. acris sensu stricto*. It is relatively constant in appearance throughout its range. Except for its rhizomes it does not resemble specimens of subsp. *friesanus* from eastern France, but it cannot be morphologically distinguished from some of the intermediate plants between subsp. *friesanus* and subsp. *acris* which occur in eastern France. The relationships of this variety are not clear; no plants of *R. acris* were seen from the region north of the Pyrenees adjacent to the area occupied by this variety.

A taxon of uncertain status is *R. steveni* Andrz. ex Bess., Enum. Pl. Volhyn., 22 (1822). The name has been much used, but with many different interpretations. Hylander (1943) suggested that the plants originally described might have been forms intermediate between *R. acris* and *R. strigulosus* or, judging from inadequate and doubtful type material, might only be *R. acris* subsp. *acris* with elongated rootstocks such as occurs when a rootstock is buried.

THE BRITISH FORMS OF *R. ACRIS*

Only *R. acris* subsp. *acris* occurs in Britain. The general cline in morphological characters of subsp. *acris* across Europe is visible even within the British Isles.

Subsp. *acris* var. *villosus* occurs in northern Scotland and Ireland, and var. *pumilus* occurs only in the Cairngorms, Scotland.

The principal former classifications of British material were those of Townsend (1900) and Drabble (1930). These, and the descriptions of *R. acris* and its varieties in British Floras up to only a few years ago, were based on adaptations of continental systems to British material, even though many of the continental forms do not occur in Britain. The varieties were chiefly delimited on the character of the rootstock and on the width of the leaf-lobes. From an examination of herbarium material determined by Drabble and other British botanists, no justification could be found for them to have called some rootstocks rhizomatous and others premorse; and the differences between the varieties in leaf-lobe width were found to be mainly due merely to seasonal variation. Plants collected in the spring were generally called var. *boreanus* or var. *multifidus*, whereas those collected in the autumn were called var. *steveni* or var. *friesanus*.

KEY TO THE EUROPEAN TAXA

Descriptions of leaves refer to those produced just before the first flowering stem of the year.

Measurements of petiole-hairs refer to the largest hairs on the petioles, excluding the sheath region. (Abnormally large hairs of rare occurrence, for any particular plant, are ignored.)

1. Rootstock much elongated, rhizomatous. Leaves on vegetative shoots arranged in two ranks
   2. Beaks of achenes distinctly hooked. Petiole-hairs frequently less than 0·8 mm in length (rarely exceeding 1·2 mm) often very fine (less than 0·02 mm wide) but plants with thicker hairs (up to 0·05 mm) common. Leaves thin, usually broadly lobed with many teeth .. .. .. *R. acris* subsp. *friesanus*
      3. Leaves broadly lobed. Petiole-hairs frequently very fine, often patent .. .. (Mainly in France and Switzerland, commonly introduced to other countries) *R. acris* subsp. *friesanus* var. *friesanus*
      3. Leaves narrowly lobed. Petiole-hairs never very fine, always appressed .. .. .. (The Pyrenees and eastern Spain) *R. acris* subsp. *friesanus* var. *pyrenaeus*
   2. Beaks of achenes straight, or only slightly curved, never hooked. Petiole-hairs long, exceeding 0·8 mm in length (frequently exceeding 1·2 mm) and thick (always exceeding 0·03 mm). Leaves thick, broadly lobed with relatively few teeth
      4. Beaks of achenes 0·5–0·7 mm. Stamens with fewer than 20 hairs/filament .. .. (Eastern Europe) *R. strigulosus*
      4. Beaks of achenes exceeding 0·8 mm. Stamens often with more than 30 hairs/filament .. .. (South Spain and Morocco) *R. granatensis*

1. Rootstock short, premorse. Leaves on vegetative shoots produced spirally .. *R. acris* L. *sensu stricto* (excluding subsp. *friesanus*)
   5. Central lobe of the median leaf-segment less than 2/5 of leaf length. Petiole-hairs deflexed, always very fine (less than 0·02 mm wide), white .. .. (Arctic coast of Russia) *R. acris* subsp. *borealis*

5. Leaves variously divided, only rarely with the central lobe of the median segment less than 2/5 of leaf length. Petiole-hairs appressed, spreading or deflexed, rarely less than 0·02 mm wide .. .. .. *R. acris* subsp. *acris*
   6. Leaves produced before the first flowering stem of the year glabrous (those produced later bearing hairs), usually shallowly lobed, never finely divided .. (Scandinavia, Iceland, Scotland (Cairngorms)) *R. acris* subsp. *acris* var. *pumilus*
   6. Leaves hairy, variously divided
      7. Hairs on the upper surface of the leaves rarely exceeding 1·2 mm. Leaves variously divided, often very finely .. .. (Widespread over most of Europe) *R. acris* subsp. *acris* var. *acris*
      7. Hairs of the upper surface of the leaves frequently exceeding 1·2 mm. Leaves never very finely divided, lobes usually broad .. .. .. (Scotland, Ireland, Iceland, Faeroes) *R. acris* subsp. *acris* var. *villosus*

DISCUSSION OF CHARACTERS

THE ROOTSTOCK

The type of rootstock in this complex, whether premorse, i.e. short and compact, or rhizomatous (Fig. 2) has previously been held as a character of primary importance. This indeed was found to be justified. Rhizomatous rootstocks occur in all plants of *R. strigulosus*, *R. granatensis* and *R. acris* subsp. *friesanus*. (However, it should be noted that in these taxa a rhizome is not always produced by the apical bud of a plant in its first season.) Compared with *R. acris* subsp. *acris*, which has a premorse rootstock, all these taxa have limited geographical distributions centred on a mountain range.

Although there is this clear separation of taxa on the type of rootstock, the only real difference between a premorse and rhizomatous rootstock appears to be in their degree of elongation and phyllotaxy. The phyllotaxy of a premorse rootstock is spiral, whereas that of a rhizome is distichous. The phyllotaxy is not altered in either case when rapid upward growth by extensive elongation of the internodes is induced by inundation with sand. All grades between a premorse rootstock and a fully-elongated rhizome occur in the array of forms intermediate between *R. acris* subsp. *acris* and subsp. *friesanus*.

The premorse rootstocks of subsp. *acris* are slightly longer in the west of Europe than in the east (Fig. 2). Unusually long rootstocks, approaching rhizomatous types in length, were found in some plants from the Shetland Islands.

THE LEAF

The leaf of *R. acris sensu lato* is palmate in shape and primarily three-lobed. These primary lobes, or 'segments', may either be shortly stalked or joined for a short distance. The three segments are further lobed, but never as far as the mid-vein. The shape as a whole was defined by measurements made on the median segment only. The measurements made were as follows:

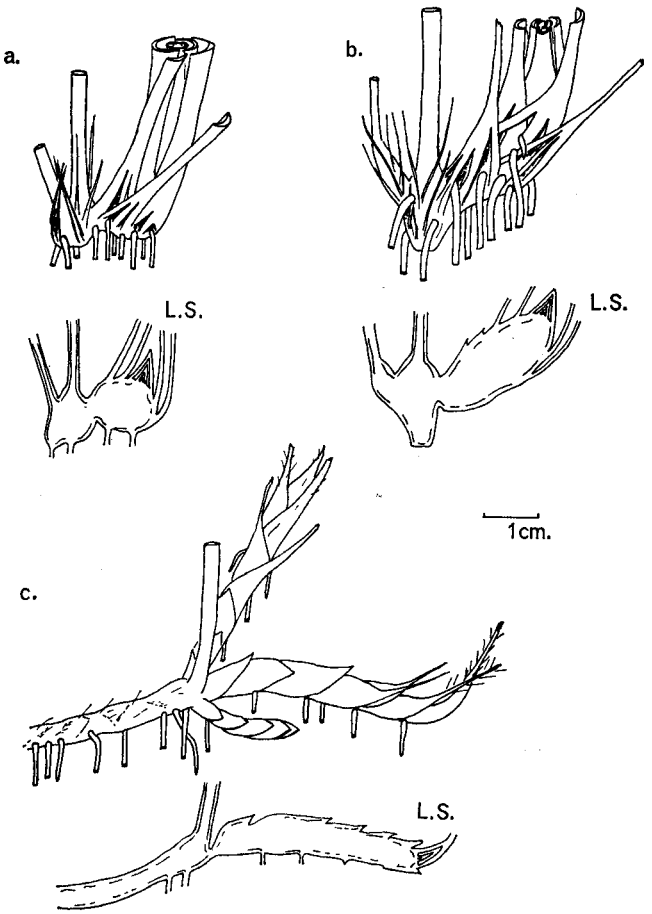

FIGURE 2. Rootstocks: showing their appearance in September.
a. & b. Premorse rootstocks of *R. acris* subsp. *acris* showing differing degrees of elongation.
a. Finland, loc. 1. b. England, loc. 62a.
c. Rhizomatous rootstock of *R. acris* subsp. *friesanus* from France, loc. 39.

L length of median segment of the leaf
X distance from base of leaf to base of the free part of the median segment
Z distance from the base of the median segment to the base of the free part of the median lobe of this segment
W width of the median lobe of the median segment, measured at the base of the free part

These measurements are shown diagrammatically in Fig. 4.

It was found, from observations of plants in cultivation, that there is a marked seasonal variation in leaf-shape. The successive leaves produced by a rosette which has overwintered show increasing dissection: those produced immediately before the first flowering stem are the most finely-dissected leaves produced during the whole year ('spring' leaves). The leaves, that are produced by the buds in the axils of these 'spring' leaves, show a marked discon-

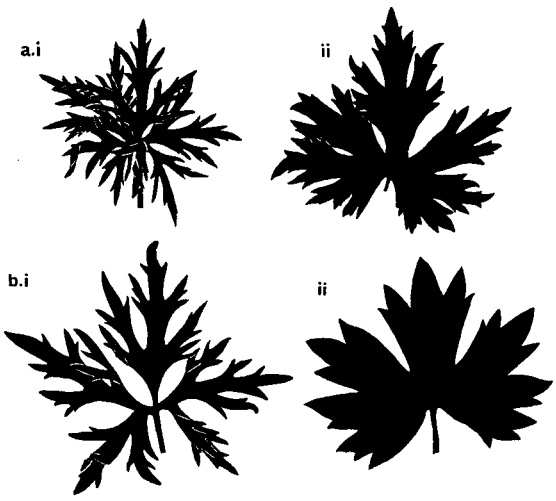

FIGURE 3. Leaf-shape.
a. Plant from England, loc. 62b: i. 'spring' leaf; ii. 'autumn' leaf.
b. Plant from Ireland, loc. 109: i. 'spring' leaf; ii. 'juvenile' leaf produced in the autumn after transplantation.

tinuity in shape, being more broadly lobed and less deeply divided ('autumn' leaves) (Fig. 3). A gradual increase in dissection of the leaves then occurs until 'spring' leaves are produced. This seasonal variation in leaf-shape has been almost totally overlooked by previous workers.

The comparisons of leaf-shape were restricted to the innermost 'spring' leaves. Leaf-shape as recorded by the ratios X/L, Z/L and W/L is shown diagrammatically in Fig. 4 for the whole of Europe. Figs. 5, 6, 7 and 8 show W/L plotted against Z/L; these two ratios are those which most closely define the

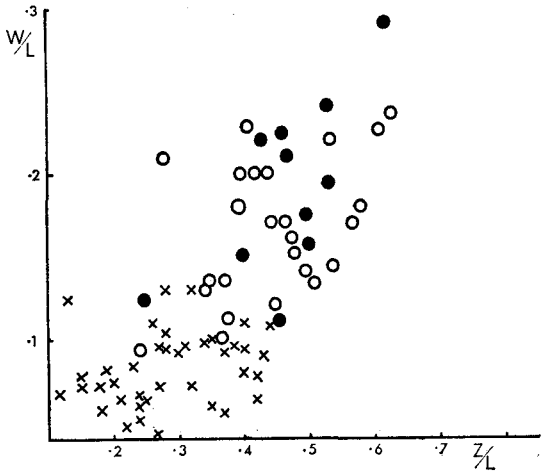

FIGURE 5. Graphical comparison of leaf-shapes. ● *R. granatensis.* × *R. acris* subsp. *acris* from E. Europe. ○ *R. strigulosus.*

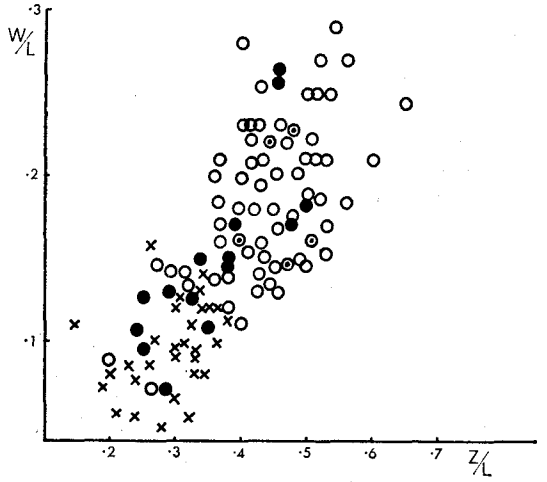

FIGURE 6. Graphical comparison of leaf-shapes.
× *R. acris* subsp. *acris* from France.
O *R. acris* subsp. *friesanus* var. *friesanus* from France, Austria, Switzerland and Sweden.
⊙ *R. acris* subsp. *friesanus* var. *friesanus* in cultivation from France, loc. 39.
● *R. acris* subsp. *friesanus* var. *pyrenaeus* from France and Spain.

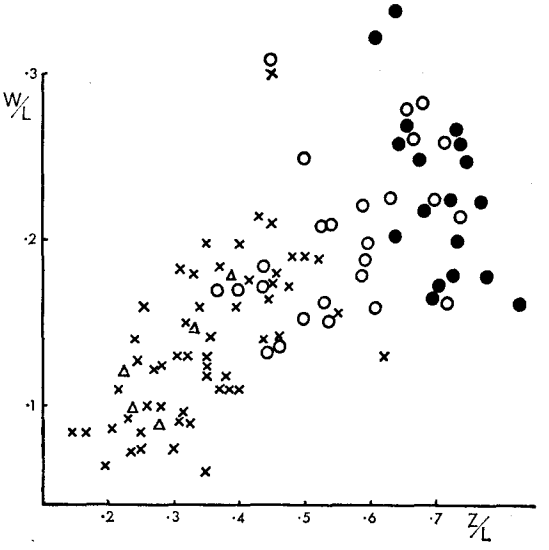

FIGURE 7. Graphical comparison of leaf-shapes.
× *R. acris* subsp. *acris* var. *acris* from Norway and Sweden.
△ *R. acris* subsp. *acris* var. *acris* in cultivation from Sweden, loc. 23.
O *R. acris* subsp. *acris* var. *pumilus* from Norway and Sweden.
● *R. acris* subsp. *borealis* from N. Russia.

major characteristics of the leaf-shapes. These figures show more clearly the range in leaf-shapes of certain groupings. Examples of actual leaf-shapes are given in Fig. 9.

R. strigulosus and *R. granatensis* are both characterised by having broad-lobed leaves. Fig. 5 shows how their range in leaf-shape is similar. On the characters of W/L and Z/L alone they appear similar in leaf-shape to some of the western European *R. acris sensu stricto*; but they differ in that although they have broad-lobed leaves the segments, especially in the case of *R. granatensis*, are often only slightly fused or even stalked and the leaves, especially in the case of *R. strigulosus*, have few teeth relative to their length. This latter feature also occurs in eastern European *R. acris* subsp. *acris*, but such leaves are always narrowly lobed. The leaves of *R. granatensis* and *R. strigulosus* are usually thicker than those of *R. acris sensu stricto*, due to the former having larger cells; this is the only anatomical difference which has been reported among the European taxa.

R. acris subsp. *friesanus* is characterised by its broad-lobed leaves, which distinguish it from subsp. *acris* as it occurs in the surrounding districts (Fig. 6); but leaf-shape alone would not distinguish it from all the forms of subsp. *acris* that are to be found in north-west Europe. Most of the overlap in leaf-shape shown in Fig. 6 is due to subsp. *friesanus* var. *pyrenaeus*, rather than to plants of subsp. *friesanus* showing introgression with subsp. *acris*.

The much wider range in leaf-shapes within plants of subsp. *acris* from north-west Europe is shown in Figs. 7 and 8. Fig. 7 also shows how the leaf-shape of subsp. *borealis* differs from that of nearly all other groups excepting some of the north Scandinavian subsp. *acris* var. *pumilus*.

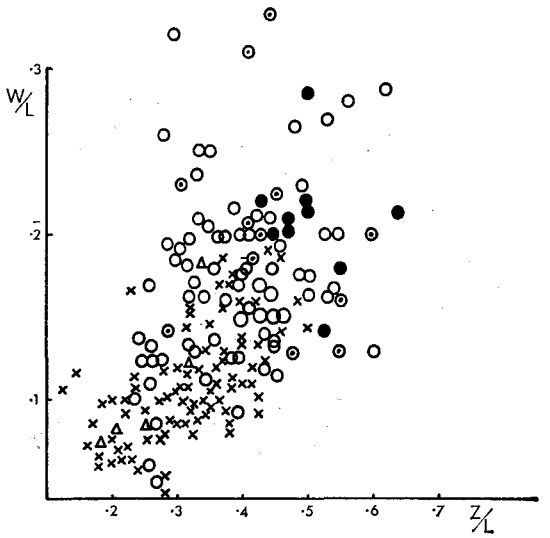

FIGURE 8. Graphical comparison of leaf-shapes.

× *R. acris* subsp. *acris* var. *acris* from England and Wales.
△ *R. acris* subsp. *acris* var. *acris* from England, loc. 62b.
○ *R. acris* subsp. *acris* var. *acris* from Scotland, Iceland and The Faeroes.
● *R. acris* subsp. *acris* var. *pumilus* from Scotland, Iceland and The Faeroes.
⊙ *R. acris* subsp. *acris* var. *villosus* from Scotland, Iceland and The Faeroes.

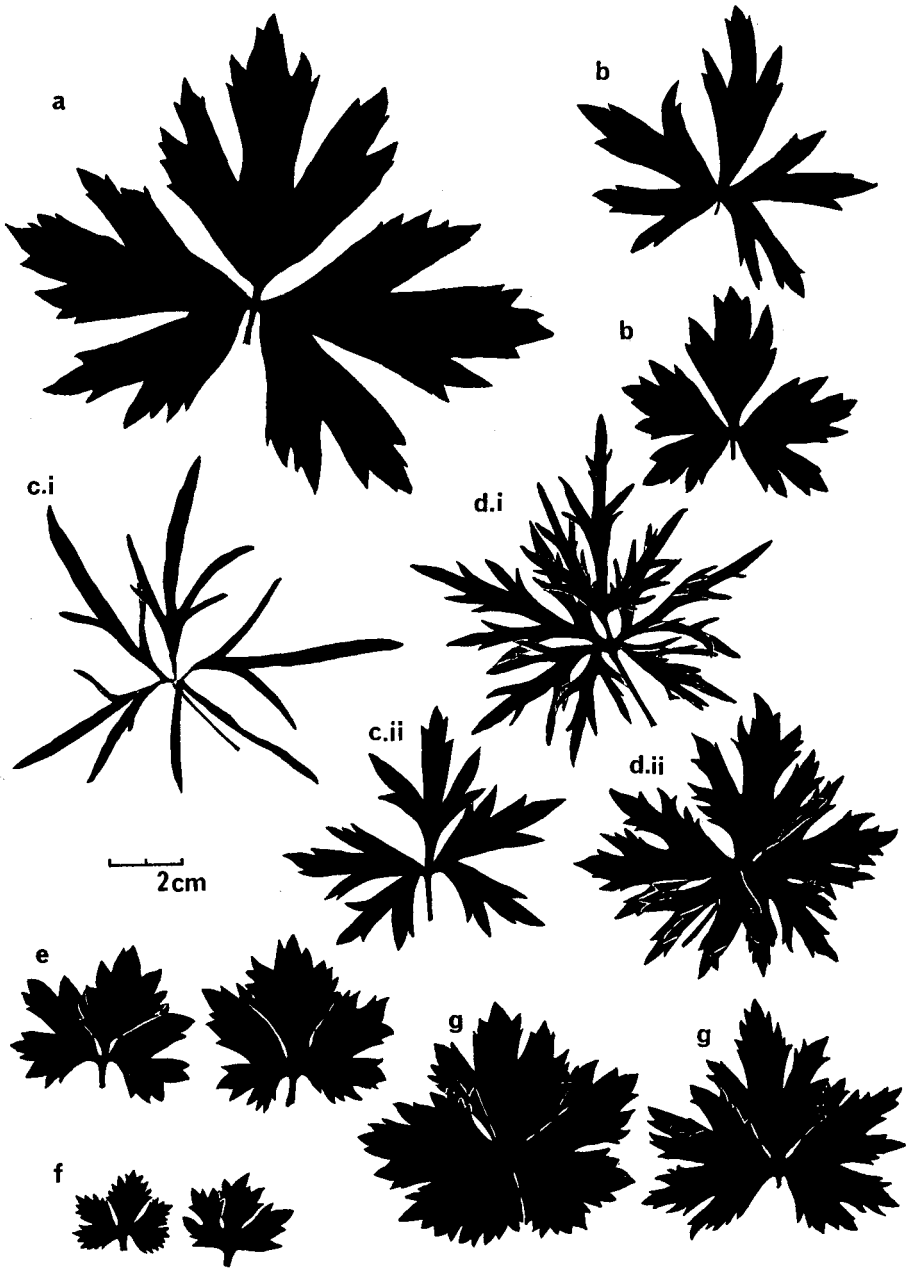

FIGURE 9. Examples of leaf-shapes.
a. *R. granatensis* – Sierra Nevada, S. Spain. b. *R. strigulosus* – Transylvania, Rumania.
c. *R. acris* subsp. *acris* from E. Europe: i. Hungary – loc. 58. ii. Austria – loc. 54.
d. *R. acris* subsp. *acris* from W. Europe: i. England – loc. 60. ii. England – loc. 73.
e. *R. acris* subsp. *borealis* – Vaigach Is., N. Russia.
f. *R. acris* subsp. *acris* var. *pumilus* – Kiruna, Sweden.
g. *R. acris* subsp. *friesanus* – Lyon, France.

THE STEM

A variable number of foliar organs occurs on the stem; the lower are stalked and similar to the basal leaves, but higher up they become sessile and simpler in form. The shapes and sizes of these organs can nearly always be correlated with those of the basal leaves, The exceptions to this correlation occur in most plants of subsp. *borealis*, subsp. *acris* var. *pumilus* and in many plants of var. *villosus*. These plants have relatively broad, little-divided leaves, but the transition to simple linear bracts is often abrupt.

The key in *Flora Europaea* (Tutin 1964) uses the height of the stem as one of the main diagnostic characters separating some of the taxa. Studies of both herbarium and cultivated material showed this to be a character of negligible value.

THE HAIRS

Plants of the complex are generally rather hairy, except in their winter state. Plants of *R. acris* subsp. *acris* var. *pumilus* are unusual in having glabrous 'spring' foliage. The pedicels of all plants always bear appressed hairs.

The hairs are single-celled and simple in form. Measurements of hair characteristics were made on the petioles (above the sheathing region) and on the lower part of the stem. The hairs were scored as appressed, spreading or deflexed. The density of hair cover was scored using four subjective categories: very dense, continuous, scattered, glabrous. The density was scored for 'spring' organs, as it usually increases on the 'autumn' organs. The maximum values of hair-length and width on the petioles were recorded (any unusually large hairs for the organ concerned were ignored). Length and width were divided into five arbitrary categories as follows:

	Length		Width
A	up to 0·4 mm	1	up to 0·02 mm
B	over 0·4 mm to 0·8 mm	2	over 0·02 mm to 0·03 mm
C	over 0·8 mm to 1·2 mm	3	over 0·03 mm to 0·04 mm
D	over 1·2 mm to 1·6 mm	4	over 0·04 mm to 0·05 mm
E	over 1·6 mm	5	over 0·05 mm

The results are shown in Figs. 10 and 11. In *R. acris* subsp. *acris* glabrous petioles and stems are rarely found except in subsp. *acris* var. *pumilus*. Glabrous stems occur mainly in the plants from areas with a continental climate or from northern mountains, whereas hairiness is associated with more oceanic climates and southern European mountains. Other trends are for longer hairs in the west rather than in the east of Europe, and for deflexed hairs to be rarely found except in the western oceanic region. Throughout the entire range of subsp. *acris* a wide range of hair-widths occurs and no geographical trends of variation are apparent, except in Scandinavia where montane plants always have relatively narrow hairs. Only very narrow hairs occur on plants of subsp. *borealis*.

In *R. acris* subsp. *friesanus* the range in length and types of hairs is similar to that of western European plants of subsp. *acris*, except that in var. *friesanus* very narrow hairs are common, and in all the plants examined of var. *pyrenaeus* the hairs were appressed.

R. strigulosus and *R. granatensis* are alike in always having very long, wide hairs.

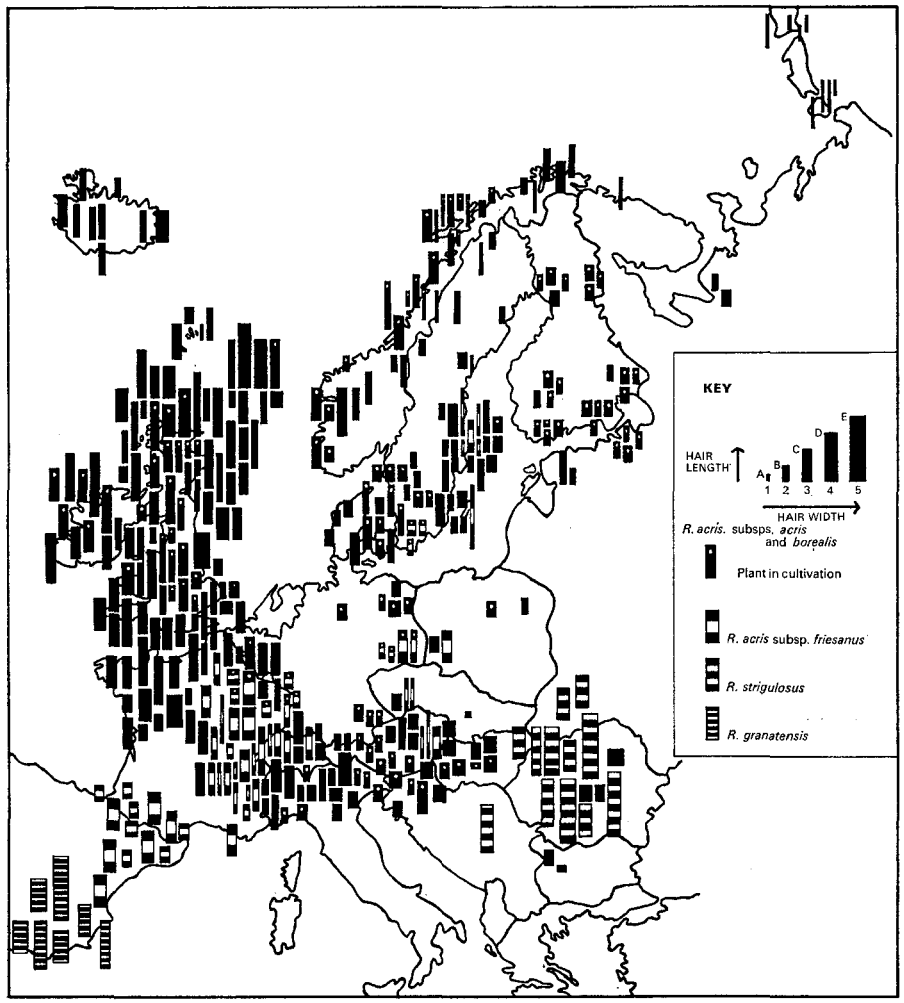

FIGURE 11. Petiole-hairs, lengths and widths.

The lengths of the hairs on the upper surfaces of the leaves are generally similar to those on the petioles; however *R. acris* subsp. *acris* var. *villosus* has hairs on the upper surface which are commonly over 1·2 mm in length, a character not found in other members of subsp. *acris*, even when such hairs commonly occur on the petioles.

In most cases the colour of the hairs appears to be closely correlated with the hair widths. The colours from the wider to the narrower hair-types range from an orangy-brown, through increasingly paler shades of fawn to white.

THE FLOWER

On the sepals of *R. acris sensu stricto* hairs of different lengths are more or less evenly distributed. In both *R. strigulosus* and *R. granatensis* the longest hairs are usually restricted to the upper two-thirds of the sepal. The zone lacking

long hairs is usually more distinct in *R. granatensis*, but sepal hair-type does not form a reliable diagnostic character separating *R. strigulosus* from *R. granatensis*.

Measurements of shape and size of petals were made on those from the earliest flowers on a cyme, since flower-size decreases later. The commonest petal-shape is broadly obovate. The only real exceptions to this are found in subsp. *acris* var. *pumilus* and subsp. *borealis*, where petals varying from very narrow to very broad occasionally occur. The shapes and sizes of the nectary-scales show great variation even from single localities; short scales tend to predominate in subsp. *borealis* and subsp. *acris* var. *pumilus*, but not to the exclusion of longer types. The petal-colour appears the same throughout the complex: the occurrence of brown-veined petals in subsp. *borealis* (Tutin 1964) is not upheld.

Most variation in petal-length is found in subsp. *acris*, where short petals occur in the east of Europe and longer ones in the west. Fig. 12 shows histograms of petal-length for groups of cultivated plants. The petal-lengths of subsp. *friesanus* are similar to western subsp. *acris*, whereas those of *R. strigulosus* and *R. granatensis* are similar to those of eastern subsp. *acris*.

Hylander (1943) reported the presence of hairs on the filaments of both *R. granatensis* and *R. strigulosus*, and stated that it thus served as a clear diagnostic character between these taxa and the rest of the complex. This is not the case, as hairs are commonly found on the filaments of eastern European *R. acris* subsp. *acris*. *R. granatensis*, however, is distinct from the rest of the complex in having

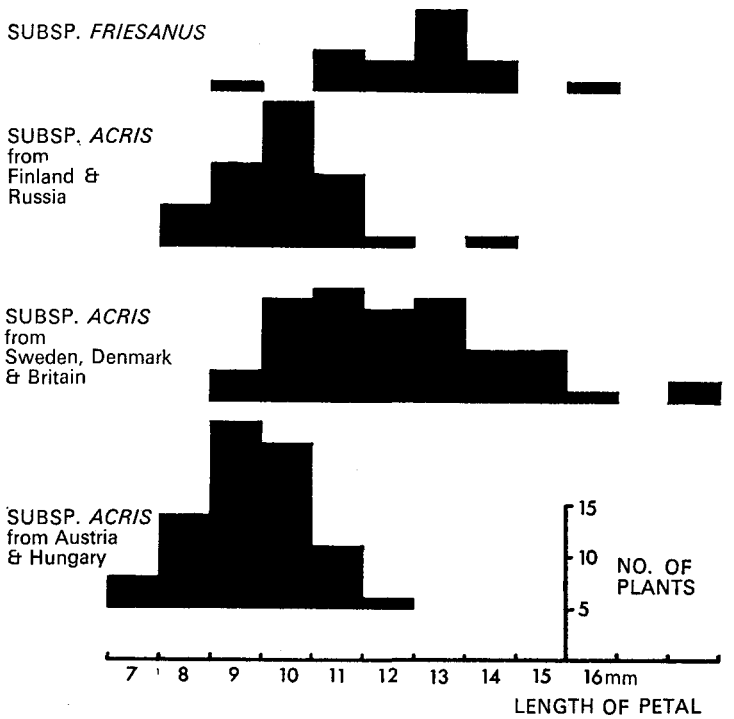

FIGURE 12. Histograms of petal-length for groups of cultivated *R. acris s.s.*

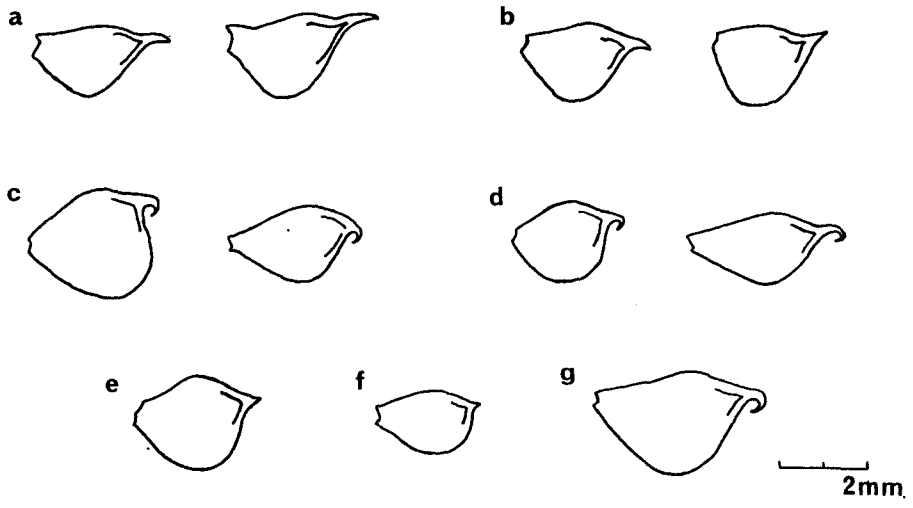

FIGURE 13. Achenes.
a. *R. granatensis* – from two plants. b. *R. strigulosus* – from two plants.
c. & d. *R. acris* subsp. *acris* from W. Europe, c. England – two plants from loc. 60.
d. Sweden – two plants from loc. 23. e. & f. *R. acris* subsp. *acris* from E. Europe,
e. Hungary – loc. 59. f. Finland – loc. 5. g. *R. acris* subsp. *friesanus* from France – loc. 41.

a greater number of hairs, at least thirty on some filaments of the flower; elsewhere it seldom exceeds twenty.

It was found that the achenes of *R. strigulosus* and *R. granatensis* are distinct from those of *R. acris sensu stricto* in having long, straight or only curving beaks, whereas in all the subspecies of *R. acris* the beaks are hooked, or very short. *R. granatensis* and *R. strigulosus* are distinct from one another in the lengths of their beaks: those of *R. granatensis* are in the range of 0·9–1·2 mm, whereas those of *R. strigulosus* are only 0·5–0·7 mm in length.

Much variation occurs in the shape and size of the achenes of *R. acris sensu stricto*. Variation in shape is often great even in plants from the same locality (Fig. 13). In general the achenes are smaller in the east of Europe and larger in the west. Achenes of subsp. *friesanus* are similar in size-range to those of western subsp. *acris*. Only immature achenes of subsp. *borealis* were seen; they appeared similar to those of western subsp. *acris*.

CHROMOSOMES AND BREEDING EXPERIMENTS

The chromosomes of *R. acris sensu stricto* have had more attention than have those of most species of *Ranunculus*. All of the more recently published counts of the chromosome number are of $2n = 14$. In the earlier counts most of the variations found in the chromosome number were reported by two workers only, Senjaninova and Sorokin. Comprehensive lists of these and other earlier counts are given by Gregory (1941) and Coonen (1939).

No chromosome counts have been reported for *R. strigulosus* and *R. granatensis*. Pollen-grain size and stomatal diameter were examined in herbarium material and were found in most cases to be greater than those in *R. acris sensu*

stricto. Although no definite conclusions can be drawn from these measurements they suggest that the first two species may possibly be polyploids.

Breeding experiments were carried out using *R. acris* subsp. *acris* and subsp. *friesanus* from a series of different localities. Compatibility of selfing and occurrence of apomixis were tested. The plants which were used were grown in a greenhouse and the flowers were individually covered with cellophane bags. In these tests, out of more than 3,500 carpels from emasculated buds only 29 seeds were set and of the 4,500 carpels which had been selfed only 3 seeds were set. For a number of reasons, the seed which was set was most probably due to contamination. It is highly probable, therefore that all plants of *R. acris sensu stricto* are obligate outbreeders. This was previously not thought to be the case (Marsden-Jones & Turrill 1935, 1952; James & Clapham 1935). Preliminary tests were made which suggest that the incompatibility mechanism is gametophytic.

The interfertility of plants from different regions and of different morphological types was tested by means of a series of test crosses. These were between plants from differing localities using mainly pollen from plants from localities 5 (Finland), 50 (Austria) and 39 (subsp. *friesanus*) (see Appendix 1 for localities). The results are given in Table 1. All the plants tested were found to be freely interfertile and the seed set between geographically remote and morphologically dissimilar plants was generally at least as good as that between morphologically similar plants from the same country. The percentage of seed set generally depended on carpel fertility rather than on the origin or fertility percentage of the pollen.

The fertility of the 'hybrid' F_1 plants was tested by examination of the meiotic divisions of the pollen-mother-cells. However, irregularities in the pairing of the chromosomes were found as frequently in the parental plants as in the hybrids. An estimate of apparent fertility of the pollen of the parent and hybrids was made by staining the pollen in cotton blue. Even parental plants of normal appearance were found commonly to have a percentage of good pollen as low as 20% and seldom more than 80%. The following list gives the percentages of good pollen in the first flower produced on a stem which had flowers of normal appearance (each value refers to a separate cultivated plant).

Loc. 62a (England) : 56, 76, 59, 83, 56, 46, 60, 75, 70, 54%
Loc. 62b (England) : 40, 24, 18, 27, 28%
Loc. 33 (Germany) : 47, 42, 35, 39, 21%
Loc. 39 (France) : 91, 89, 70, 73, 67%
Loc. 22 (Sweden) : 79, 53, 80, 79, 75%

The first flower was always taken, as the percentage of good pollen fluctuates greatly among different flowers of the same plant; even percentages as measured above can vary greatly from season to season.

DISCUSSION AND CONCLUSIONS

Measurements of characters were made on organs produced at apparently the same season and at the same position on the plant, so that they would be comparable. This restricted the number of characters that could be measured on much of the herbarium material. Seasonal variation in leaf-shape had been ignored by most of the previous workers on this complex.

The presence or absence of a rhizome was found to be a reliable diagnostic

TABLE 1. TEST CROSSES BETWEEN CULTIVATED PLANTS OF WILD ORIGIN

Results expressed as percentage seed set per flower.

	♂ Parents														
Locality numbers	5	50	39	1	2	4	6	24	22	62b	32	33	41	40
1	79; 68	82; 91; 76	61; 67; 95					92				94	94	
2	54; 96 76	69; 61; 60	85; 63					85 46						
3	92; 96	93; 90	96; 92											
4	54; 91	54; 86	88; 21; 87					34	22					
5		87; 79; 61	70; 73; 64					29						
6	0;8	94; 29; 50 61	94; 29; 28 43; 68											
8	78; 83	90; 79	78; 91											
25	66; 59	88; 90	73; 72											
23	76; 81	72; 89	91;67											
24	73; 58	90; 77; 65	43; 47			59								
22	63; 61	65; 67	78; 73											
62b	12; 17	9; 11; 32 17; 27	12; 0; 6 17											
50	86; 84		78; 74; 35 23; 94; 83 92; 88; 87	93 83		19	94	77		70	90 87	91 61		85
58	56; 67	48; 82	81; 90							53 72				
48	95; 84	84; 73	94; 89							85 77				
44	42; 21	28;23	29; 10; 47 21							38				
32	83; 72 78	63; 84; 91	98; 95; 80 91; 89; 79	74 46 86								90 75		
33	41; 37	52; 93; 24	41; 0; 45		23 69	66								
39	63; 87	36; 14; 0 0; 68; 63												
41	52; 36	54; 65	39; 48							28				
40	63; 65	48; 74; 41 85	57; 54; 56 73; 75							70 64				

character. Leaf-shape was found to be diagnostic for most taxa, although it was very variable even within plants from a single locality. Hair-type was similarly found to be very variable in some localities, but most taxa were characterised by hairs of a particular length and width. Differences in floral characters were found between the three species, but within *R. acris sensu stricto* no taxa could be delimited on such characters.

Chromosome number is constant within *R. acris sensu stricto* ($2n=14$). All plants within *R. acris sensu stricto* appear freely interfertile, but information as to the fertility of plants resulting from such crosses, compared with that of the parental plants, would require a detailed knowledge of factors controlling femaleness. Although femaleness is so common it would appear disadvantageous to the species, which is an obligate outbreeder. It is suggested that there is a possibility that *R. granatensis* and *R. strigulosus* may be polyploids, but no living material of these two species was available.

All the rhizomatous taxa within the complex appear to have evolved in the mountainous regions of southern Europe. *R. granatensis* and *R. strigulosus* show so many features in common that presumably they must have come from a common stock. *R. acris* subsp. *friesanus*, which also has rhizomes, shows no close relationship to either of these species.

An array of intermediate plants were found between the different morphological forms within *R. acris sensu stricto*. This can be attributed to the facts that all the plants of this species appear to be obligate outbreeders, there appear to be no sterility barriers between any forms of the species, and the ecological or geographical barriers, which must have occurred especially in the case of subsp. *friesanus*, appear to be breaking down due to farming activities, which also enable the plants to spread as weeds.

ACKNOWLEDGMENTS

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I also wish to thank the curators of the herbaria, from which material was loaned, and the many people who helped collect living material.

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APPENDIX 1

ORIGIN OF PLANTS TO WHICH REFERENCE IS MADE

1	Espoo, Finland	40	Strasbourg, France
2	Borgå, Finland	41	Massif de Hoheck, Vosges, France
3	Tampere, Finland	44	Udine, Italy
4	Punkaharju, Finland	48	Genova, Italy
5	Kuusamo, Finland	50	Graz, Austria
6	Oulu, Finland	54	Heiligenblut, Austria
8	Leningrad, Russia	58	Budapest, Hungary
22	Landskrona, Sweden	59	Dorog, Budapest, Hungary
23	Göteborg, Sweden	60	Church Stretton, Shropshire, England
24	Värnamo, Sweden		
25	Stockholm, Sweden	62	Cawston, Warwickshire, England
32	Gransee, E. Germany	73	Middleton-in-Teesdale, Durham, England
33	Karlmarxstadt, E. Germany		
39	Mairon-sur-Bèze, Dijon, France	109	L. Mask, Co. Mayo, Ireland

APPENDIX 2

EXAMPLES OF HERBARIUM MATERIAL OF THE RECOGNISED TAXA

R. strigulosus Schur (Fig. 14A)

In pratis Transsilvan., *D. J. Schur* (**W**)

Transsilvanica, Hermannstadt, 12. VI. 1906, *J. Barth* (**W**)

Tilalmas prope Toroczko, Transsilvanica, VII. 1883, *J. de Csató* (**P**)

Kolozsvar, comit Kolozs, 14. V. 1916, *M. Péterfi* (**C**)

R. granatensis Boiss. (Fig. 14B)

Sierra Nevada, sunny bank by the bridge over R. Genil . . . , 10. VI. 1926, *A. J. Wilmott* (**BM**)

In Valle fluv Feint, Nevada, 29. VI. 1876, *M. Winkler* (**C, W**)

Sierra de Segura, above Rio Segura near La Toba, edge of water channel, 27. VI. 1955, *V. H. Heywood* (**LTR, LIVU**)

Sierra Nevada, lot. humidus graminos in Dehesa de S. Gerorimo et valle fl. Monothil, 9. VIII. 1879, *Huter* (**CGE, C, E, S**)

R. acris L. subsp. *acris* var. *acris* (Fig. 15A)

Beaminster, Dorset, 2. VI. 1913, *I. M. Roper* (**CGE**)

Austria Inferior, In pratis ad 'Mauer' prope 'Wien', VI. 1903, *E. v. Halácsy* (**W**)

Rossica, Archangelsk extra oppidum . . . , 13. VII. 1911, *S. J. Enander* (**S**)

R. acris subsp. *acris* var. *pumilus* Wahlenb. (Fig. 16A)
Lycksele Lappmark, Tärna, Norra Storfjället, Daláive, 31. VII. 1944, *H. Lenander* (S)
Torne Lappmark, Jukkasjärvi parish, Mt. Atjaktjåkko, 5. VIII. 1947, *H. Smith* (E)
Corrie-an-Lochan, East side of Braeriach, E. Inverness, 12. VIII. 1898, *E. S. Marshall* (CGE)

R. acris subsp. *acris* var. *villosus* (Drabble) S. M. Coles (Fig. 15B)
Melvich, W. Sutherland, 15. IX. 1897, *W. A. Shoolbred* (BM, CGE, LTR)
Coast near Rockfield, E. Ross, 19. VII. 1890, *E. S. Marshall* (CGE)
Near the summit of Langa, Harris, 14. VIII. 1841, – (CGE)

R. acris subsp. *borealis* (Trautv.) Nyman (Fig. 16B)
Novaya Zemlya, Matotschin Schar, 30. VII. 1908, *R. Niemann* (CGE)
Waigats Is., Dolga Bay, 1–10. VII. 1897, *H. W. Fielden* (CGE)
Waigatsch, sinus Warnek, 11. VIII. 1902, *O. Ekstam* (S)

R. acris subsp. *friesanus* (Jord.) Rouy & Fouc. var. *friesanus* (Fig. 17A)
Lyon à Chanelay, *A. Jordan* (CGE)
Forêt du Rhin-du Bois, Cher, 2. VI. 1855, *A. Déséglise* (P)
Near Archettes, Forêt d'Epinal, Vosges, 30. VII. 1963, *E. K. Horwood* (LTR)

R. acris subsp. *friesanus* var. *pyrenaeus* S. M. Coles (Fig. 17B)
Prov. Teruel. Albarracin, lieux humides et herbeux, sur le calcaire 1,300 m, VI. 1894, *E. Reverchon* (BM, E, P, S)
Guipuzcoa. Gabo de Higuer, V. 1895, *M. Gandoger* (C)

FIGURE 14

A. *R. strigulosus* Schur
[In pratis fertilibus, Transsilvan. . . ., —. VI. –, D. J. Schur (W).]

B. *R. granatensis* Boiss.
[Sierra de Castril. . . . –. VII. 1903, E. Reverchon (E).]

FIGURE 15

A. *R. acris* L. subsp. *acris* var. *acris* [D'Angers, 18. VI. 1853, A. Jordan (C).]

B. *R. acris* L. subsp. *acris* var. *villosus* (Drabble) S. M. Coles [Damp ground sloping to a small rocky bay, Nr. Melvich, W. Sutherland, Ref. No. 1864, 15. VII. 1897, E. S. Marshall (CGE).]

FIGURE 16

A. *R. acris* subsp. *acris* var. *pumilus* Wahlenb. [Lule Lappmark, Kvikkjokks Kapellförs. . . ., 23. VII. 1943, S. Selander & N. Dahlbeck (S).]

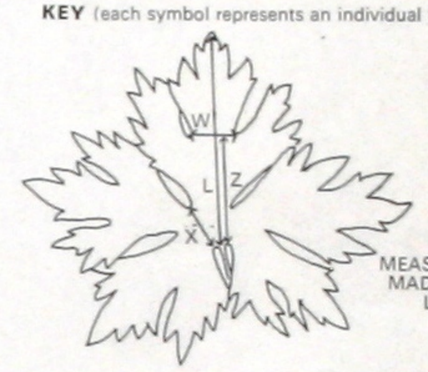
B. *R. acris* subsp. *borealis* (Trautv.) Nyman [Novaja Semlja, Matotschkin Scharr., 20. VIII. 1891, O. A. Ekstam (S).]

FIGURE 17

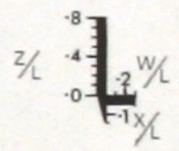
A. *R. acris* subsp. *friesanus* (Jord.) Rouy & Fouc. var. *friesanus* [Lyon à Chanelay, Herb. Jordan (CGE).]

B. *R. acris* subsp. *friesanus* var. *pyrenaeus* S. M. Coles [Nr. Hospice de France, Haute Garonne. . . ., 26. VII. 1961, E. K. Horwood (LTR).]

KEY (each symbol represents an individual plant)



MEASUREMENTS MADE ON THE LEAVES



Leaf-segments sessile

Leaf-segments stalked

Plant in cultivation (other measurements made on herbarium material)

R.granatensis

R.strigulosus

R.acris subsps. *acris* and *borealis*

R.acris subsp. *friesanus*

Figure 4

LEAF - SHAPE

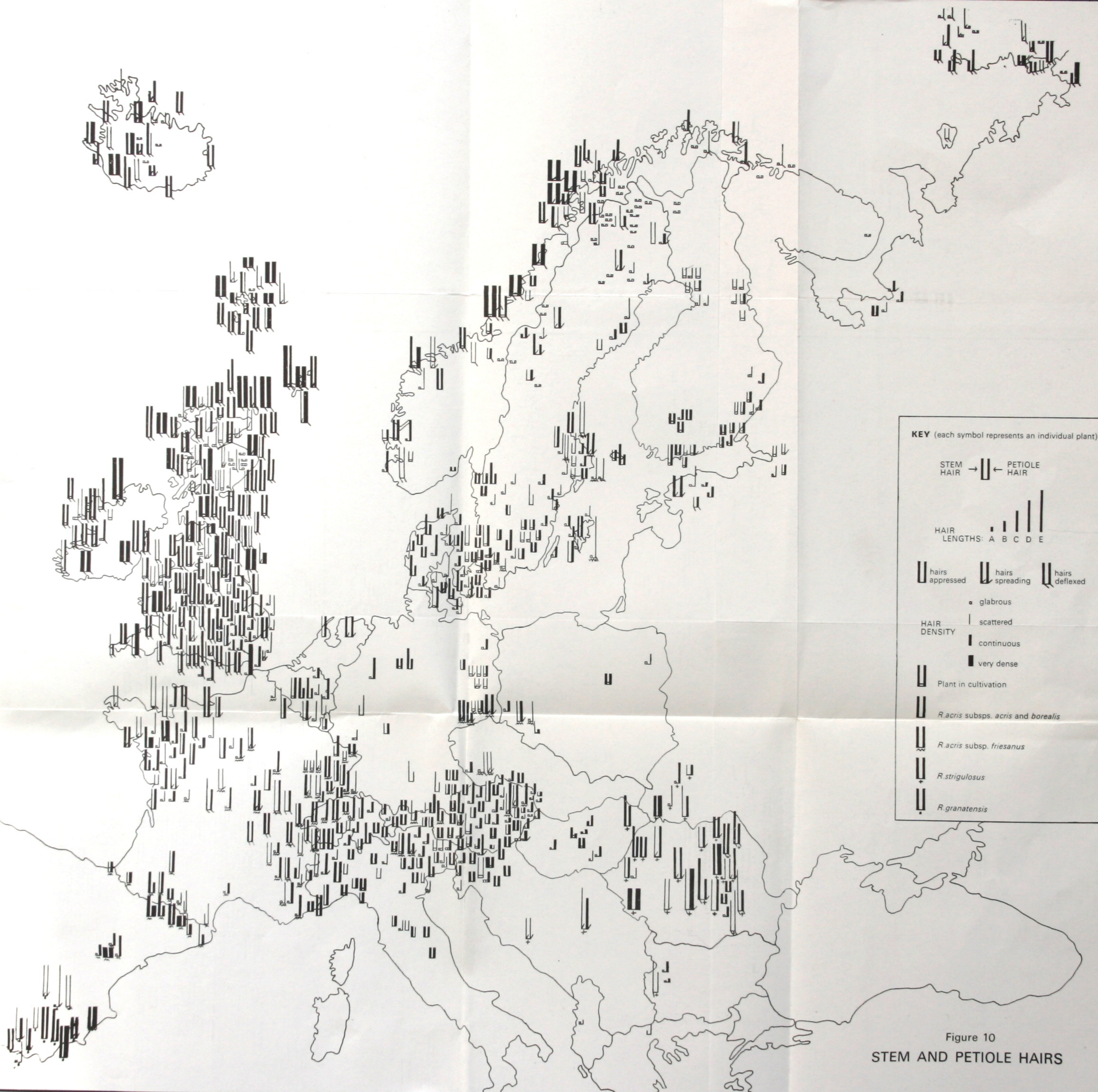


Figure 10

STEM AND PETIOLE HAIRS